Beetlemania: is the bark worse than the bite? Rocky Mountain subalpine forests recover differently after spruce beetle outbreaks and wildfires

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1   ***Abstract.*** Due to the shifting global climate, the frequency and severity of disturbances are

2   increasing, inevitably causing an increase in disturbances overlapping in time and space. Bark

3   beetle epidemics and wildfires have historically shaped the disturbance regimes of Western

4   North American forests. Their interactive effects on stand dynamics and recovery are

5   inadequately studied in *Picea engelmannii* (Engelmann spruce)-*Abies lasiocarpa* (subalpine fir)

6   dominant forests; understanding these interactions is imperative to the management and health of

7   forested ecosystems. This study focuses on the effects of epidemic *Dendroctonus rufipennis*

8   (spruce beetle) outbreaks, high-severity fires, and the subsequent species and structural diversity

9   of subalpine forest regeneration and structure in Northern Colorado and Southern Wyoming. We

10   compared tree seedling densities and species composition, surface fuel loading, and stand

11   structure characteristics across 80 sites that experienced either high tree mortality from epidemic

12   spruce beetle outbreaks (>50% affected basal area), high-severity wildfire, post-outbreak high-

13   severity wildfire (1-3 years post-outbreak), or no disturbance (control). The beetle outbreak sites

14   span multiple years post-outbreak from 1996-2017, ultimately comprising a chronosequence of

15   beetle-affected stands. Analyses indicate a significant increase in fuel loading over time-since-

16   outbreak, as aerial fuels are transferred to the forest floor following high tree mortality. Tree

17   seedling densities among outbreak and control sites differ significantly from burned areas,

18   indicating that wildfires override the effects of repeated disturbances on regeneration. There is

19   consistent Engelmann spruce seedling survival following beetle outbreaks, providing evidence

20   for stable forest recovery following a single disturbance. However, fire was a dominate force in

21   determining post-disturbance species composition, indicating continued prevalence of high

22   severity fire may prove detrimental for the persistence of spruce-fir species, while promoting

23   shifts toward more drought and fire tolerant tree species (e.g., *Pinus contorta*). It is critical to

24 understand post-disturbance fuel dynamics and stand recovery to identify hazards for subsequent

25 fire suppression, implement treatments to enhance forest resilience, and to understand the

26 potential consequences of climate-induced shifts in disturbance regimes on forest health.

27 *Key words: disturbance ecology; bark beetle; wildfire; fuels; subalpine forest; regeneration;*

28 *forest health*

29 **INTRODUCTION**

30   Subalpine forests are dominant in high-elevation or cold temperature sites across western

31 North America. This far-reaching ecosystem historically experienced infrequent high severity

32 disturbances, including wildfires and bark beetle outbreaks (Kulakowski et al. 2003; Veblen

33 2000). High-severity disturbances, such as wildfires and bark beetle outbreaks, are drivers of

34 subalpine forest succession and composition, and fuel accumulation and changes. These

35 disturbances have shaped these ecosystems for millennia, but increasing disturbance extent in

36 recent years has led to concerns about post-disturbance recovery and the potential interacting

37 effects of these biotic and abiotic disturbances.

38   High severity disturbances in subalpine ecosystems historically occurred on the century

39 scale and have predominantly been driven by climate (Bessie and Johnson 1995). Wildfires in

40 these forests are relatively infrequent, typically high-severity or stand-replacing occurring at

41 intervals of 300-600 years (Romme and Knight 1981; Veblen 2000; Schoennagel et al. 2004).

42 Fire exclusion in subalpine forests has had minimal effects on historic fire regimes, particularly

43 in the Rocky Mountains due to fire return intervals that span centuries (Romme and Despain

44 1989; Sherriff et al. 2001). Unlike forests at lower elevations, subalpine forests are not fuel

45 limited; fires in subalpine forests are climate-driven and are often associated with drought

46   conditions (Sherriff et al. 2001). Meanwhile, historic spruce beetle (*Dendroctonus rufipennis*)

47   outbreaks varied in severity, with high-severity outbreaks occurring at intervals of 100-250 years

48   over the past several centuries (Veblen 2000). Dendrochronological reconstructions have shown

49   that drought conditions have driven historical outbreaks and that recent epidemic bark beetle

50   outbreaks were preceded by warmer temperatures (Hart et al. 2014; Hebertson and Jenkins

51   2008). In addition, reconstructions have shown widespread synchronicity of outbreaks,

52   indicating a regional driver, such as climate (Hart et al. 2014). Climate change may be altering

53   the disturbance regimes of both wildfire and bark beetle outbreaks in these systems with

54   documented evidence of increasing fire season length, greater burn areas, and even more fire

55   starts (Abatzoglou and Williams 2016; Dennison et al. 2014; Schoennagel et al. 2017;

56   Westerling et al. 2006). Changes in climate may also play a role in the extent and severity of

57   bark beetle outbreaks in subalpine forests (Hart et al. 2014; Dell and Davis 2019).

58   These two disturbances significantly alter fuel complexes over time with large

59   implications on subsequent disturbances. High-severity wildfires alter fuels both through

60   consumption of burnable fuel and the creation of new dead fuels. Due to the severity of

61   subalpine wildfires, postfire surface fuels consist of coarse woody debris and downed logs. Slow

62   decomposition rates contribute to the persistence of postfire surface fuels on the landscape for

63   decades to centuries. Similarly, bark beetle caused mortality may have long-lasting impacts on

64   forest structure, stand recovery, and future disturbances. Canopy and surface fuel components

65   can change dramatically as the Engelmann spruce (*Picea engelmannii)* move from the "yellow

66   phase" (1-3 years after bark beetle attack) when needles lose foliar moisture content, to the "gray

67   stage" (3-10 years after attack) when needles and fine branches fall, to the "old stage" (10+ years

68   after attack) when standing dead snags fall to the forest floor (Andrus et al. 2016). The

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69   conversion of standing trees to downed logs is associated with an accumulation of combustible

70   and often continuous coarse woody surface fuel loads (Stephens et al. 2018). Additionally,

71   several studies found that higher elevation surface fuels tend to be denser and more continuous

72   than other forest types, contributing to characteristic stand-replacing fires in subalpine forests

73   (Taylor and Fonda 1990; Fryer and Johnson 1988). Outbreak severity, rate of mortality, and

74   spatial arrangement of host trees within a stand can further influence the alteration of fuel

75   complexes throughout space and time in beetle-affected stands (Hoffman et al. 2015; Sieg et al.

76   2017). The effects of bark beetle caused mortality on fire behavior varies greatly throughout

77   evolving outbreak stages (Hoffman et al. 2015; Sieg et al. 2017); the variable impacts of fuel

78   moisture and spatial arrangement at the time of burning are important concerns for land

79   managers and fire managers to consider.

80   In addition to changes in fuels complexes, spruce beetle outbreaks and wildfires alter

81   regeneration dynamics and species recovery. Following the loss of mature Engelmann spruce

82   trees, species dominance shifts toward subalpine fir. Post-outbreak recovery depends on the

83   release of tree regeneration already present on site, taking decades for Engelmann spruce to

84   attain basal area dominance (Veblen et al. 1991). On the other hand, species recovery following

85   stand-replacing wildfires requires seed dispersal from unburned area for new recruitment cohorts

86   (Veblen et al. 1991). Lodgepole pine and quaking aspen quickly and prolifically colonize burned

87   subalpine stands. Serotinous lodgepole pine relies on an aerial seedbank for seed dispersal, and

88   quaking aspen is able to resprout from extensive root systems that can survive high-severity fires

89   (Mitton and Grant 1996; Harvey et al. 2016). Engelmann spruce preferentially establishes on

90   bare mineral soil, allowing early, but slow, postfire recruitment (Johnstone and Chapin 2006).

91   Due to litter layer requirements for establishment, subalpine fir is typically one of the last species

92   to colonize a post-fire landscape (DeRose & Long 2010; Harvey et al. 2016). As postfire

93   recovery develops, spruce and fir attain basal area dominance over shade-intolerant lodgepole

94   pine and quaking aspen and become climax community dominants. While lodgepole pine and

95   quaking aspen are fire- and drought-tolerant species, spruce and fir seedlings are particularly

96   sensitive to postfire moisture stress and large burn patches, slowing their postfire recovery

97   following large fires and droughted conditions (Coop et al. 2010; Harvey et al. 2016). This has

98   important implications for the future of subalpine stands; altered disturbance regimes and

99   changing climatic conditions create uncertainty about the persistence of spruce-fir forests.

100   Furthermore, it is unknown how these forests will respond to both spruce beetle and wildfire

101   disturbances, requiring further investigation.

102   Few studies in recent literature have analyzed the potential of compounded disturbance

103   effects on conifer regeneration in the Rocky Mountains (Carlson et al. 2017; Harvey et al. 2013;

104   Harvey et al. 2014*a*; Kulakowski et al. 2013; Stevens-Rumann et al. 2015). In upper montane

105   mixed-conifer forests, Harvey et al. (2014*a*) found that pre-fire beetle outbreaks can reduce post-

106   fire regeneration if outbreak severity is high enough to diminish seed sources. However, in these

107   lodgepole pine dominated stands, viable seeds of serotinous cones can persist in the aerial

108   seedbank, contributing to post-fire regeneration despite pre-fire outbreaks (Harvey et al. 2014*a*).

109   In dry mixed-conifer forests dominated by Ponderosa pine (*Pinus ponderosa*) and Douglas-fir

110   (*Pseudotsuga menziesii*), Stevens-Rumann et al. (2015) found no compounded effects from bark

111   beetle outbreaks and wildfire on post-disturbance regeneration, while in similar systems Harvey

112   et al. (2013) found compounded effects on regeneration following high-severity beetle outbreaks

113   coupled with low-severity fire, due to a reduction of pre-fire *in situ* seed sources. Finally, in

114   subalpine forests, Carlson et al. (2017) found that there may be a reduction in post-fire tree

115   regeneration due to pre-fire spruce beetle outbreaks. This effect of linked disturbances on post-

116   fire regeneration was attributed to differences in vegetation recovery because of post-outbreak

117   surface fuel effects on fire behavior (Carlson et al. 2017). The effects of multiple disturbances on

118   post-disturbance recovery varies by forest type and disturbance severity. Although most studies

119   have indicated that climate has a critical impact on post-disturbance regeneration, there is

120   considerable uncertainty in the literature regarding the nature of bark beetle-fire interactions and

121   associated regeneration dynamics.

122   This study focused on the effect of spruce beetle outbreaks, high-severity fires, and their

123   interactive effects on subalpine forests in Northern Colorado and Southern Wyoming, USA. We

124   constructed a chronosequence of beetle-affected stands in various post-outbreak stages in order

125   to analyze how fuels change over time following the spruce beetle epidemic. We chose to focus

126   on outbreaks that occurred from 1996 until 2017 due to the resulting widespread mortality from

127   these events, as well as widespread discrepancies in the scientific literature on interacting

128   disturbances and recovery dynamics in these systems. The goals of this study were to answer the

129   following questions: 1) how does time-since-outbreak affect stand and fuel structures in

130   subalpine forests? 2) how does the recovery trajectories and fuel complexes differ between

131   wildfires, outbreaks, or a combination of the two disturbances? and 3) what are the site-specific

132   drivers of post-disturbance fuels and tree regeneration?

133   **METHODS**

134   *Study Area*

135   Subalpine forests range in latitude from southern Canada to New Mexico, typically

136   directly below the tree line. The subalpine zone in the Central US Rockies is characterized by

137 warm, dry summers and cool, wet winters, with the majority of annual precipitation in the form

138 of snow. These forests commonly consist of long-lived shade-tolerant species such as

139 Engelmann spruce and subalpine fir (*Abies lasiocarpa)*, and to a lesser extent quaking aspen

140 (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*) at earlier seral stages.

141   Study sites were located in northern Colorado and southern Wyoming in subalpine forests

142 in the Arapaho-Roosevelt National Forests, Routt National Forest, and Medicine Bow National

143 Forest (Figure 1). Sites were located in subalpine stands at a range of elevations from 2,591 to

144 3,326 meters above sea level and were predominately composed of Engelmann spruce and

145 subalpine fir, and to a lesser extent quaking aspen and lodgepole pine. On average, study sites

146 received 97.03 centimeters of precipitation per year, ranging from 48.77 to 115.32 centimeters

147 over the timespan of the outbreak under study (USDA NRCS 2020). The average temperatures

148 for study sites range from a mean low of -8.11° C to a mean high of 13.83° C (USDA NRCS

149 2020). A large-scale (5,261 ha (13,000 ac)) blowdown event occurred in 1998 in the Hahns

150 Peak/Bears Ears Ranger District of the Routt National Forest in northern Colorado (Schaupp et

151 al. 1999). This event initiated spruce beetle infestations in healthy, standing Engelmann spruce

152 trees, triggering a landscape-scale epidemic outbreak, which had been exacerbated by warmer

153 and drier conditions.

154 *Site Selection*

155   We used Aerial Detection Survey (ADS) data of spruce beetle outbreaks that have

156 occurred from 1996 to 2017 collected by the USDA Forest Service, Forest Health Protection and

157 its partners, to identify areas with beetle caused mortality (USFS 2017). ADS data is collected

158 from an aircraft, from which the collector manually indicates forest changes on a map. Due to

159 this methodology's nature, bark beetle outbreaks are not detected until after the tree needles start

160   to fade and change color. Therefore, there is typically a 1-3 year lag between initial infestation

161   and detection through aerial surveys; thus we used the year of initial detection above 10% tree

162   mortality as the outbreak year. We also used Monitoring Trends in Burn Severity (MTBS) data

163   on wildfires in spruce-fir forests (MTBS Data Access 2017).

164   ArcMap (10.6) was used to generate random points within outbreak polygons across a

165   gradient of time-since-outbreak, as well as within burned areas. Outbreak plots were defined as

166   >50% of stand basal area (m^2/ha) affected by spruce beetle. We used MTBS data to map high-

167   severity fires since 1996, as well as post-outbreak high-severity fires. All plots were located at

168   least 50 meters from any trail or road. Both severity and bark beetle mortality were field verified.

169   The outbreak plots were categorized into five different groups based on the year the

170   outbreak was detected: 1996-2004, 2005-2008, 2009-2010, 2011-2014, 2015-2017. Post-

171   outbreak fire sites were sites where a spruce beetle outbreak was detected 1-3 years prior to a

172   high-severity wildfire (Burn Ridge Fire, 2002; Hinman Fire, 2002; Wolverine Fire, 2005) and

173   high-severity fire sites were burned in 2002 without previously detected outbreaks (Big Fish

174   Fire, Lost Lakes Fire, Hinman Fire). Control plots were defined as <25% stand basal area

175   colonized and/or dead. Ten sites were established in each of the five outbreak groups as well as

176   in high-severity burn sites, post-outbreak fire sites, control sites for a total of 80 plots with equal

177   representation in each group. This chronosequence of outbreaks represents the spread of

178   epidemic outbreaks over time; the earliest outbreaks started in the Routt National Forest and

179   subsequently spread to the Medicine Bow National Forest, Arapaho National Forest, and

180   Roosevelt National Forest. Due to the time from infestation to detection, as well as the

181   progressive nature of outbreaks (in that all trees at a particular site likely did not die in the same

182   year), the "year of outbreak" is somewhat of an estimate; we used outbreak time groups to

183   address this. All data was collected in the summers of 2018 and 2019, resulting in a

184   chronosequence of 1 to 21 years post outbreak sites, while post-outbreak fire sites and high-

185   severity burn sites were measured 14-17 years post-fire.

186   *Sampling Design*

187   We modeled our plot design after Ott et al. (2018), establishing 0.08-ha circular fixed

188   area plots. Topographic characteristics were collected at each plot, using smartphone Global

189   Positioning System for elevation and aspect collection and a clinometer for slope collection.

190   Within each plot, measurements were taken for each standing tree ($\geq$ 12.7cm diameter at breast

191   height (DBH)). Species, DBH, crown base height (on living trees), tree health, spruce beetle, and

192   other insect impacts were recorded. Tree health was ranked on a scale from 1 to8 to quantify

193   live, dead, or dying status (modified from Forest Inventory and Analysis National Core Field

194   Guide, USDA 2017). We used live basal area as a proxy for canopy cover. Standing Engelmann

195   spruce trees were flagged or tagged for future monitoring. Pre- and post-disturbance basal area

196   and density was calculated by species.

197   We established four 16.1m long transects within each fixed area plot that extended in the

198   cardinal directions from the plot center. Following Brown (1974), we tallied woody surface fuels

199   in 1- (<0.6cm), 10- (0.6-2.5cm), and 100-hour (2.5-7.6cm) size classes along the transects. 1-

200   hour fuel data were collected for seven meters on each transect. 10- and 100-hour fuels were

201   counted along the entire length of the transects (16.1m). A total of 20 litter and duff depths were

202   taken along the four transects. Point intercept sampling was employed along each transect for a

203   total of 100 points to identify life forms of understory growth (shrub, forb, graminoid, tree) and

204   the corresponding substrate (litter, woody debris, moss/lichen, rock, bare ground).

205   We established two types of subplots. For 1000-hour fuels (≥7.6cm) (coarse woody

206   debris), we established 0.015-ha (6.9m radius) circular subplots located at the plot center. We

207   measured end diameters and length of each downed log; if a log extended outside of the subplot,

208   we took the end diameter at subplot edge. We modeled transect sampling lengths and the coarse

209   woody debris subplot area after Sikkink and Keane (2008) to bolster plot representativeness. To

210   quantify tree regeneration, we established five 0.004-ha (3.6m radius) subplots: one center

211   subplot and one at the end of each transect. In each regeneration subplot, we counted and

212   classified all tree regeneration (any living tree <2m height) by height and species.

213   *Statistical Analyses*

214   Statistics and graphics were completed in R (R Core Team 2019). To answer question

215   one, we used a simple linear model (Gaussian family) to analyze the effect of time since

216   outbreak on different forest structural parameters, including overstory mortality, stand structure,

217   and fuel loading (Table 1). The presence of insect mortality agents other than spruce beetle was

218   negligible in all sites and was not included in analyses. To answer question two, we used one-

219   way analyses of variances (ANOVAs) using disturbance groups as the predictor variable with

220   similar response variables as those to answer question one. Tukey-adjusted comparisons were

221   used to compare ANOVA groups using the emmeans package in R (Lenth 2019). There was no

222   observed change in total seedling densities, Engelmann spruce seedling densities, nor subalpine

223   fir seedling density across outbreak groups (F<0.7, P>0.40). For this reason, analyses on seedling

224   densities were performed on disturbance type (bark beetle, post-outbreak fire, high severity fire,

225   control) rather than across the chronosequence of time since outbreak in both ANOVAs and

226   GLMs by species.

227   For question three, generalized linear models (GLM; Gaussian family) were used to

228   assess site specific drivers on seedling density by species, stand structure characteristics, and fuel

229   complexes. Aspect was transformed using Beer's transformation for analyses. The control group

230   was used as the reference for the disturbance groups in the GLM analyses. Individual models

231   were developed for different tree seedling species; all significant predictors were incorporated

232   into larger, inclusive generalized linear models. Due to differences in life history traits,

233   corresponding live standing densities were included in the GLM analyses for drivers of

234   lodgepole pine and quaking aspen regeneration.

235   We tested the assumptions that these sites were comparable by assessing pre-outbreak

236   basal area. We included all bark beetle killed stumps to retroactively composite a pre-outbreak

237   basal area and performed an ANOVA to assess differences in basal area among disturbance

238   groups. We assessed the assumptions of normality and variance with Shapiro-Wilks and

239   Levene's tests. Due to the widespread variability within and among groups of seedlings, log-

240   transformed seedling densities were used in analyses in order to satisfy normality assumptions

241   for ANOVA and regression models. Due to the clustering of plot locations, we also tested

242   assumptions of autocorrelation among plots by including it as a factor in a generalized linear

243   mixed model; it represented less than 1% of the variance and thus was excluded. A threshold of

244    $\alpha=0.05$ was used to designate statistical significance, and each study plot was a sample unit

245   (N=80).

246   **RESULTS**

247   Across all post-outbreak sites, mean pre-outbreak basal area was 60.5 ± 19.6 m^2/ha, with

248   Engelmann spruce and subalpine fir as codominant overstory. Lodgepole pine and quaking aspen

249   made up 2.48% and 0.60% of pre-disturbance density, respectively. Pre-disturbance basal area

250   were similar across groups (F=1.34, P=0.268). Beetle-affected trees (either dying or dead,

251   hereafter referred to as snags) ranged from 50% to 96% of plot basal area, with an average of

252   65% affected plot basal area. The quadratic mean diameter of beetle-killed trees was

253   41.7±10cm.

254   *Time-since-outbreak influences stand structure and fuel complexes*

255   Time-since-outbreak significantly impacted many fuels and stand structure

256   characteristics. The abundance of standing Engelmann spruce snags was lowest in the oldest

257   outbreak group (1996-2004) and highest in the intermediate outbreak group (2009-2010)

258   (F=4.742, P=0.003). Sites in the youngest outbreak groups had moderate levels of standing

259   Engelmann spruce snags (Figure 2). The proportion of standing live Engelmann spruce density in

260   plots decreased with increasing time-since-outbreak. In control sites and newly infested bark-

261   beetle sites, live standing Engelmann spruce dominated stand density over subalpine fir. In the

262   oldest outbreak sites, live Engelmann spruce density dropped by as much as 94% compared to

263   pre-outbreak Engelmann spruce density (F=60.714, P<0.0001). Beetle-killed trees begin to fall

264   ~8-9 years following spruce beetle outbreak detection (R^2=0.142, P=0.007). This corresponded

265   to an increase in dead woody surface fuels, especially in the larger size classes (Figure 3).

266   Total downed woody fuel loading increased with time-since-outbreak (Figure 3e). This

267   relationship was not observed in 1-hour fuels but is apparent in all other fuel size classes (Figure

268   3a). Woody fuels in the 10-hour, 100-hour, and 1000-hour size classes all have a positive linear

269   relationship with increasing time-since-outbreak (Figure 3b, c, d).

Disturbance type impacts of forest structure and fuels

270   Total fuel loading is highest in the oldest outbreak group (1996-2004) and the high-

271   severity fire group (F=4.85, P<0.001, Figure 4a). 1-hour fuel loading is lowest in high-severity

272   burn sites and highest in the oldest outbreak site (F=2.66, P=0.02). Fuels in the 1-hour size class

273   are similar across control, post-outbreak fire, and recent outbreak groups (Appendix Figure 1).

274   10-hour fuel loading is greatest in oldest outbreak sites, which is not statistically different than

275   10-hour fuel loading in either burn group (F=4.61, P<0.001; Appendix Figure 1). 10-hour fuel

276   loading is significantly lower in recent outbreak and control groups compared to the oldest

277   outbreak sites. Fuels in the 100-hour size class were greatest in the oldest and post-outbreak fire

278   sites but were not statistically different in the intermediate outbreak and high-severity burn

279   groups. The lowest 100-hour fuel loading was found in the two most recent outbreak groups and

280   control sites (F=5.283, P<0.001; Appendix Figure 1). Similarly, coarse woody debris fuel

281   loading (1000-hour size class) was highest in the oldest outbreak and the high-severity burn

282   group but were not statistically different in the intermediate outbreak years, post-outbreak fire,

283   and control groups (F=4.52, P<0.001; Appendix Figure 1). Coarse woody debris makes up a

284   large proportion of total downed woody fuel loading; the patterns observed in 1000-hour fuels

285   mirror total woody fuel loading trends.

286   Understory vegetation cover remained consistent across groups, showing no relationship

287   with increasing time-since-outbreak. Similarly, litter and duff depths remained constant across

288   outbreak groups but were significantly reduced in burned groups (F=2.96, P=0.009; 2.47,

289   P=0.02). Litter depth is highest in control sites (mean=2.95cm) and lowest in high severity fire

290   and post-outbreak fire sites (1.37cm and 1.66cm, respectively) (F= 2.96, P=0.009). Duff depths

291   are lowest in both burn groups (mean depth of 3.2cm-3.6cm) and highest in outbreak and control

292   groups (mean depth of 6.1cm-7.0cm) (F=2.47, P=0.02).

293   Tree seedling densities were significantly reduced in both burn groups (F=6.31,

294   P<0.0001) (Figure 4b). Seedling densities in outbreak and control groups were not statistically

295   different from each other (F=9.17, P<0.0001). Engelmann spruce seedling densities in control

296   sites are statistically similar to burn groups and bark beetle sites (Figure 5a). Subalpine fir

297   seedlings are significantly lower after wildfire and post-outbreak fire than in bark beetle and

298   control sites (F=15.52, P<0.0001; Figure 5b). Subalpine fir seedling densities are statistically

299   similar in bark beetle and control sites. Engelmann spruce seedling densities are significantly

300   lower in both burn groups than in bark beetle sites (F=5.29, P=0.002). However, this pattern of

301   seedling densities was not observed for other species, such as lodgepole pine and quaking aspen

302   regeneration, that comprised a smaller proportion of tree seedling densities across our sites.

303   Lodgepole pine seedling densities are either lowest or absent in bark beetle sites, and highest in

304   post-outbreak fire sites (F=6.66, P<0.001). Lodgepole pine seedling densities in high-severity

305   fire and control sites are not statistically different than bark beetle or post-outbreak fire sites

306   (Figure 5c). Quaking aspen regeneration densities are lowest in bark beetle sites and highest in

307   post-outbreak fire sites (F=3.49, P=0.02). Similar to lodgepole pine, quaking aspen regeneration

308   densities in high-severity fire and control sites are not statistically different from bark beetle or

309   post-outbreak fire sites (Figure 5d).

310   *Site specific drivers of forest structure*

311   Elevation (P=0.15), aspect (P=0.44), and slope (P=0.28) were not significant in

312   predicting total woody fuel loading when experimental groups are included in the model (Table

313   1). The oldest outbreak group (P=0.01) and high-severity fire group (P=0.003) were both

314   positively correlated with total woody fuel loading relative to the control group. Elevation

315   (P=0.16), aspect (P=0.83), slope (P=0.16), and group were not correlated with 1-hour fuel

316   loading. Elevation was negatively correlated with woody fuel loading in the 10-hour size class

317   (P=0.002). Aside from correlations with time-since-outbreak and burn groups described above,

318   neither aspect (P=0.85) nor slope (P=0.47) were correlated with woody fuels in the 10-hour size

319   class (table 2). Similarly, elevation had a negative correlation with fuels in the 100-hour size

320   class (P=0.0006). Aside from correlations with disturbances, neither aspect (P=0.67) nor slope

321   (P=0.33) had significant correlations with woody fuel loading in the 100-hour size class. Finally,

322   aside from correlations with disturbances, there were no significant abiotic predictors of woody

323   fuels in the 1000-hour size class (elevation: P=0.22; aspect: P=0.43, slope: P=0.31; Appendix

324   Table 1).

325   For each species, disturbance type was a significant predictor of seedling densities

326   (P<0.009) (GLM, Appendix Table 2). Additionally, live basal area was strongly correlated with

327   total seedling density (F=17.23, P<0.0001). Live basal area, used as a proxy for canopy cover,

328   was not included in the GLM analyses due to the correlation between live trees and disturbance

329   type.

330   Similar trends were observed in both dominant subalpine species. Disturbance type was

331   the only significant variable correlated with Engelmann spruce seedling density. High-severity

332   fire (P=0.006) and post-outbreak fire (P=0.009) were both negatively correlated with Engelmann

333   spruce seedling densities (Appendix Table 2). Live basal area was strongly correlated with

334   Engelmann spruce seedlings; greater live tree coverage was correlated with higher seedling

335   densities (P=0.001). Contrary to our expectations, elevation (P=0.77), aspect (P=0.38), slope

336   (P=0.17), and total fuel loading (P=0.68) were not correlated with Engelmann spruce seedling

337   densities. Similarly, disturbance type was the only significant predictor of subalpine fir

338   seedlings; high-severity fire (P<0.0001) and post-outbreak fire (P<0.001) groups were negatively

339   correlated with subalpine fir densities. Elevation (P=0.90), aspect (P=0.57), slope (P=0.30), litter

340   cover (P=0.74), and total woody fuel loading (P=0.36) were not correlated with subalpine fir

341   seedling densities. Live basal area had a strong positive correlation with subalpine fir seedlings

342   (F=20.45, P<0.0001).

343   Different predictors were observed for lodgepole pine and quaking aspen seedling density

344   (Appendix Table 2). As elevation increased, lodgepole pine seedling density decreased

345   (P=0.009) and similarly as total woody fuel loading increased, lodgepole pine seedling density

346   declined (P=0.05). Disturbance type and standing lodgepole pine density (P<0.004) were both

347   positive predictors of seedling densities. Specifically, post-outbreak fire (P=0.002) sites were

348   positively correlated with lodgepole pine regeneration. Similarly, elevation was the only negative

349   predictor of quaking aspen regeneration (P=0.002); there were fewer regenerating aspen at

350   higher elevations. Disturbance type and standing aspen density were positively correlated with

351   aspen regeneration density (P<0.0001 for both). Both high-severity fire (P=0.006) and post-

352   outbreak fire (P<0.001) sites were positively correlated with quaking aspen regeneration

353   densities.

354   **DISCUSSION**

355   Forest disturbances, such as bark beetle outbreaks and wildfires, leave ecological legacies

356   that can influence the occurrence and behavior of future disturbances (Johnstone et al. 2016).

357   This study improves our understanding of the recovery trajectories following bark beetle

358   outbreaks, wildfires, and overlapping disturbances, within 1-21 years following these

359   disturbances. Post-outbreak fuel loading, across all size classes except 1-hour fuels, increased

360   linearly with time-since-outbreak. Similarly, high fuel loads accumulate substantially after high-

361   severity wildfires. High post-disturbance fuel loads and their lasting effects will persist on the

362   landscape for decades into the future. Subalpine tree seedling densities were significantly lower

363   following wildfires than bark beetle outbreaks, with no observed evidence of compound effects

364   from multiple disturbances on tree seedling densities. Tree seedling densities were consistent

365   over time-since-outbreak, indicating that beetle-affected stands will slowly recover to spruce-fir

366   dominated forests in the absence of fire.

367   *Forest composition*

368   The abundance of Engelmann spruce snags initially increased as beetles successfully

369   killed host trees and were initially identified as "dying" but not fully dead, and then decreased

370   with increasing time-since-outbreak as trees fell and accumulated as woody surface fuels. The

371   greatest density of standing snags were present 6-9 years after spruce beetle outbreak, before

372   snags began to fall, which is similar to post-outbreak structural changes in other forest types such

373   as Douglas fir and Ponderosa pine dominated systems (Negrón et al. 2009; Hoffman et al. 2012;

374   Donato et al. 2013; Jenkins et al. 2014).

375   The loss of host trees in beetle-affected stands resulted in an increase of subalpine fir

376   percent composition over time-since-outbreak. This creates subalpine fir-dominated stands until

377   Engelmann spruce regeneration matures into the canopy (Veblen et al. 1991). In stands

378   unaffected by bark beetles, Engelmann spruce had stand density dominance over subalpine fir.

379   However, species dominance switched to favor subalpine fir with increasing time-since-

380   outbreak. This switch in species dominance can result in long-term changes to subalpine forest

381   structure if there is reduced Engelmann spruce regeneration as expected with warming and

382   drying conditions (Lazarus et al. 2017). Consistent with other studies on post-outbreak subalpine

383   structure in different geographic areas, we observed higher subalpine fir tree regeneration

384   densities in most bark beetle stands, though Engelmann spruce was still a component of the

385   regeneration (DeRose and Long 2010). The reduction in mature Engelmann spruce trees will

386   shift host tree size distribution to smaller size classes and decrease stand susceptibility to

387   subsequent spruce beetle infestations for as long as 60 years (Hart et al. 2015)

388   *Fuel complexes*

389   Constructing a chronosequence of changing fuel structures over time allowed us to

390   substitute space for time and study the effect of spruce beetle outbreaks through time in the

391   Rocky Mountains. Others have used this method in examining fuel complex changes following

392   wildfires, but not outbreaks (e.g. Roccaforte et al. 2012, Stevens-Rumann et al. 2020). As

393   expected, there was an overall increase in total downed woody fuel loading with increasing time-

394   since-outbreak. The highest woody fuel loading was in the oldest outbreak site. This correlation

395   was not observed with 1-hour fuel loading, nor was the expected peak in fine woody fuels

396   observed with the onset of the "gray stage" (Andrus et al. 2016; Jenkins et al. 2012). This is

397   likely due to the high spatial variability of 1-hour fuel loading in subalpine forests. Subalpine

398   forests are characteristically dense; the continual loss of fine twigs from the overstory to the

399   forest floor could obscure any initial pulse in 1-hour fuel loads. Additionally, these forests have

400   very slow rates of organic matter turnover and decomposition, leading to consistent

401   accumulation of fine woody fuels over time (Meyer 2013). For the 10-hour fuel loads, there was

402   a larger increase in fuel loading, ~17 years after outbreak detection. At this point in post-

403   outbreak recovery, beetle-induced fuel accumulation was distinct from background variability in

404   fine woody fuel loading. There was a gradual increase in 100-hour fuel loading after ~8 years

405   post-outbreak detection. This is consistent with the end of the "gray stage," transitioning into the

406   "old stage" of post-outbreak recovery. This trend was observed in 1000-hour fuel loading as

407   well, as standing dead trees begin to fall ~10 years after outbreak detection and continue to fall

408   as more years pass; this finding is consistent with post-outbreak treefall in Douglas-fir and

409   Ponderosa pine forests as well (Donato et al. 2013; Hoffman et al. 2012). This pattern in the

410   larger fuel size classes drove total downed woody surface fuel loading for the post-outbreak

411   trajectory of subalpine stands, contributing to a marked increase in total fuel loading 10 years

412   following outbreak detection. Due to the slow decomposition rates characteristic to subalpine

413   stands, accumulated downed woody surface fuels from bark beetle outbreaks will persist on the

414   landscape for decades to a century (Mietkiewicz et al. 2018).

415   As time passes after a spruce beetle outbreak, standing snags are transferred to dead

416   surface fuels. This causes canopy fuels to be discontinuous as live interconnecting canopy fuels

417   are reduced. There are still ladder fuels that maintain connectivity between fuel complexes due to

418   dense, suppressed regeneration that makes up the understory and subcanopy of subalpine forests.

419   This change in fuel distribution throughout the fuel layers is not expected to enhance the risk of

420   fire spread due to reduced canopy bulk density and fuel continuity, although increased wind

421   penetration can override these effects (Black et al. 2013; Jenkins et al. 2008; Sieg et al. 2017).

422   Instead, fire spread is likely to change from wildfires that predominately spread throughout the

423   crown to surface fires with long residence times (Donato et al. 2013). Standing snags also pose a

424   risk to firefighters as snags fall, especially if they become fire weakened. Thus, it is important to

425   allocate human resources carefully in these bark beetle affected areas, especially 6-9 years post-

426   outbreak, when snag fall rates begin to accelerate.

427   Wildfires in subalpine stands left greater total woody surface fuel loads on the landscape

428   than control stands; this study is one of very few recent publications to document post-fire fuel

429   characteristics in Rocky Mountain subalpine stands. These burned sites had greater proportions

430   of 100- and 1000-hour fuels, while 1- and 10-hour fuels were unchanged compared to control

431   sites. Burned sites had high coarse woody debris loads because low intensity surface fires will

432   have high-severity effects in subalpine stands, as Engelmann spruce and subalpine fir are thin-

433   barked species that are easily killed by fire (Starker 1934). Up to 100% overstory mortality led to

434   significant tree fall and coarse woody debris accumulation 14-17 years post-fire. While few

435   recent studies document post-fire fuel loads in subalpine stands, our findings were consistent

436   with Romme (1982), who found that high post-fire fuel loads in subalpine forests were mainly

437   comprised of fire-killed stems, which can take decades to centuries to decompose. Abundant

438   litter and 1-hour fuels contribute to initial fire spread, while coarse woody debris and duff layers

439   can perpetuate smoldering and soil heating effects (Romme 1982). However, we did not see litter

440   and duff depths similar to control sites even 14+ years after wildfires and 1-hour fuels were

441   similar to control sites. Some hypothesize that following a wildfire, it could take up to 100 years

442   for these fine fuel layers to develop from litterfall (Romme 1982). Consequently, recently burned

443   stands may have reduced susceptibility to subsequent fires or beetle outbreaks for 100 years or

444   more (Kulakowski and Veblen 2007).

445   Woody surface fuel loads in post-outbreak fire sites were similar to high-severity burned

446   sites and were significantly higher than fuel loads in recent outbreak and control sites. This could

447   be due to the consumption of downed fuels from beetle-killed trees. However, the post-outbreak

448   fire sites analyzed in this study capture fires that occurred 1-3 years after the bark beetle

449   outbreak. At this stage after the outbreak, snags had likely not yet begun to fall and substantial

450   coarse fuels had not accumulated. Additional data on fires that occurred in later stages of

451   outbreak recovery may provide different conclusions about compounded disturbances on fuel

452   complexes and subalpine tree regeneration. Although, numerous empirical studies have found

453   weak or non-significant relationships between beetle-kill fuels and subsequent fire severity in

454   terms of canopy mortality, increased coarse woody surface fuels from beetle-killed trees may

455   result in extended smoldering over a larger surface area, increased heat release from surface

456   fires, and detrimental impacts on soil health (Brown et al. 2003; Certini 2005; Harvey et al.

457   2014*a*; Carlson et al. 2017). Assessing heating effects on soils was beyond the scope of this

458   study given the long time-since fire considered in this study. Further studies in subalpine forests

459   are needed to understand the influence of increased fuel loads due to spruce beetle outbreaks on

460   burning conditions, high residence times, soil heating effects, and ultimately plant community

461   responses.

462   *Tree regeneration*

463   Total tree seedling densities were similar among outbreak groups and controls. This trend

464   was observed in Engelmann spruce and subalpine fir seedling densities as well. Seedling

465   densities in the oldest outbreak group are consistent with densities in the newest outbreak group.

466   The lack of significant differences in tree seedling densities across the chronosequence of beetle-

467   affected stands could be due to the shade tolerant nature of Engelmann spruce and subalpine fir.

468   Subalpine tree species do not need canopy openings for seedling establishment, which differs

469   from the tree regeneration response after bark beetle outbreaks in other forest types (Hawkins et

470   al. 2013; Collins et al. 2011). Conversely, canopy cover was a significant predictor of subalpine

471   tree seedlings, as shaded, moist microclimate conditions favor subalpine fir and Engelmann

472   spruce. Both species can persist in the subcanopy or understory for many years. This role of

473   overstory trees as facilitators of subalpine species seedling survival in spruce beetle-affected

474   stands is consistent with recent studies in subalpine stands of southwestern Utah (Pettit et al.

475   2019). Although the spruce beetle outbreaks observed in this study were high-severity

476   disturbances, there were still some live mature Engelmann spruce remaining in or nearby

477   affected stands. Middle-aged, cone bearing Engelmann spruce that have not been killed by

478   spruce beetles will continue to produce seeds, allowing for early cohorts of Engelmann spruce

479   tree seedlings in beetle-affected stands, though the quantity of seed fall has certainly changed

480   following outbreak. This indicates that the sampled outbreak stands will continue to persist as

481   spruce-fir forests. However, there is not an observed increase in subalpine tree regeneration over

482   time-since-outbreak. These findings of low post-outbreak tree regeneration are consistent with

483   Carlson et al. (2020) and may be attributed to reduced snowpack and increased moisture deficits

484   observed in western subalpine forests (Andrus et al. 2018; Lazarus et al. 2017). Ultimately, we

485   are unable to fully assess the true dynamics of subalpine tree regeneration without aging every

486   seedling that was measured. Insight into establishment dates through dendrochronological

487   techniques may clarify the difference between suppressed advanced regeneration and post-

488   outbreak recovery in these stands (Schapira et al. in preparation). Assessing the tree seedling data

489   as it is now, these stands will continue to regenerate as spruce-fir forests in the absence of large

490   fire events.

491   Engelmann spruce and subalpine fir seedling densities were dramatically reduced in both

492   burn groups compared to outbreak and control groups. However, subalpine tree seedling

493   densities were similar after high-severity burns and post-outbreak burns. There was no evidence

494   of compounded effects from multiple disturbances on subalpine tree species regeneration. This

495   finding is consistent with studies in subalpine forest types (Kulakowski et al. 2013), as well as

496   other forest types in the Rocky Mountains (Harvey et al. 2014*b*; Stevens-Rumann et al. 2015).

497   Wildfires in subalpine stands are characteristically severe; viable seed sources within burn

498   patches are limited, if existent at all. Recolonization of the burned area will depend on seed

499   delivery and establishment from unburned Engelmann spruce and subalpine fir seed sources,

500   which can be impeded by large burn patch sizes (>150m to live seed source), reduced soil

501   moisture and climatic water deficit from warming conditions (Andrus et al. 2018; Harvey et al.

502   2016). Harvey et al. (2016) documented significantly reduced Engelmann spruce and subalpine

503   fir post-fire establishment associated with severe post-fire drought conditions. Reforestation of

504   burned subalpine stands may take decades to centuries (Rodman et al. 2019) as subalpine tree

505   species have episodic seed production dependent on climatic conditions (Beuchling et al. 2016).

506   If subalpine burned areas were to reburn at higher frequencies than the system is historically

507   adapted for, there may be major shifts in forest structure. Repeated burns in subalpine forests can

508   reduce material legacies (e.g., coarse woody debris) that facilitate seedling survival, increase

509   patch sizes that reduce seedling establishment, and kill off subalpine tree species before seed

510   production (Coop et al. 2010; Harvey et al. 2016*a*; Harvey et al. 2016*b*; Turner et al. 2019).

511   Climate-induced fire regime shifts can result in unprecedented conversions of subalpine forested

512   ecosystems to non-forested systems.

513   Conversely, lodgepole pine and quaking aspen regeneration densities were highest after

514   spruce beetle outbreak and fire. Lodgepole pine seedling establishment was dependent on pre-

515   disturbance stand structure; if viable seed sources are present, post-fire conditions favor

516   lodgepole seedling recruitment due to exposed mineral soil, lack of shade by other seedlings, and

517   light seeds that can be dispersed easily by wind (Harvey et al. 2016; Johnstone and Chapin

518   2006). Additionally, lodgepole pine is a drought tolerant species; post-fire seedling establishment

519   is unaffected by post-fire drought (Harvey et al. 2016). Quaking aspen regenerates prolifically

520   after high-severity fires, through which other seedlings that may compete for light availability

521   are removed. Quaking aspen have underground root systems that can remain viable for hundreds

522   of years despite aboveground tree mortality (Peet 2000). This vegetative life strategy allows

523   aspen to resprout after high-severity fires, quickly attaining stand dominance while other conifers

524   may be reduced due to dispersal distances, post-fire climate, and reduced soil moisture. The

525   climatic predictions of increased high-severity fires in subalpine stands will favor aspen

526   dominance (Kulakowski et al. 2013). Additionally, given the serotinous nature of lodgepole pine,

527   repeated fires can perpetuate lodgepole pine dominance (Harvey et al. 2016). However, the

528   proportion of serotiny across all of our sites is unknown and highly variable. There were fewer

529   quaking aspen regeneration and lodgepole pine seedlings at higher elevations, which

530   corresponded with fewer overstory aspen and lodgepole pine trees. However, climate change

531   models predict range shifts upward in elevation; furthermore, faster range shifts in high elevation

532   ecotones are expected relative to lower elevation forests (Kroiss and HilleRisLambers 2015). A

533   warming climate coupled with changing disturbance regimes may result in unprecedented losses

534   to subalpine tree species.

535   Contrary to other studies in subalpine forest types (Andrus et al. 2018; Coop et al. 2010;

536   Harvey et al. 2016), we did not observe any effect of elevation, aspect, nor slope on subalpine

537   climax species seedling densities. This could be because cool and moist growing conditions were

538   pervasive throughout the subalpine stands that were sampled. Plots were not established on the

539   range edge of the subalpine zone, which may explain why we did not observe the expected trend

540   of Engelmann spruce and subalpine fir moving upward in elevation with warming climates

541   (Kroiss and HilleRisLambers 2015). Moreover, abiotic factors may have a weakened effect on

542   seedling densities as warming conditions hinder seedling survival. Seedlings from the

543   experimental groups of this study have been destructively sampled and aged using

544   dendrochronological techniques, in order to pinpoint establishment dates (Schapira et al. in

545   preparation). These ages will provide a clear understanding of how, or if, subalpine stands are

546 recovering from these disturbances. Data on distance to seed source may elucidate structural

547 drivers of seedling establishment. Long term, post-disturbance climate data may elucidate broad-

548 scale drivers of reduced seedling establishment.

549 *Management Implications*

550   Forest managers can implement different tactics to mitigate detrimental consequences of

551 shifting and interacting disturbance regimes. Fuel treatments within the first decade of outbreak

552 detection can reduce total fuel accumulation caused by beetle-killed overstory trees. This may

553 reduce residence times and prolonged smoldering during subsequent burning, mitigating

554 detrimental impacts on soil health and seedling establishment (Carlson et al. 2017; Certini 2005).

555 In addition, accumulated woody surface fuels and slow decomposition rates can reduce plant-

556 available soil nitrogen and impede vegetation growth; fuel treatments that remove downed logs

557 from the landscape will improve soil fertility (Edburg et al. 2012). However, prescriptions for

558 fuel treatments depend on management objectives. If managing for fire behavior, removal of

559 large beetle-killed trees and ladder fuels within the first decade of an outbreak may be beneficial.

560 However, special consideration should be given to fine fuel accumulation that has been found to

561 accumulate after salvage logging, as fine surface fuels may increase the risk of surface fire

562 spread (Donato et al. 2013*b*). Additionally, there may be negative repercussions of fuel

563 treatments on wildlife habitat. For example, the Canada lynx selectively use outbreak stands with

564 large diameter trees, and its prey, the snowshoe hare, prefers understory connectivity in

565 subalpine stands (Squires et al. 2020). In addition, small mammals, such as the red-backed vole

566 (*Clethrionomys gapperi*), selectively use areas with abundant coarse woody debris (Ucitel et al.

567 2003). Fuel reduction treatments aimed at reducing fire behavior may have negative implications

568 for listed wildlife species. If managing for resistance, proactive landscape scale removal of large

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569   diameter host trees may improve stand resistance to epidemic bark beetle outbreaks (Jenkins et

570   al. 2014; Temperli et al. 2014) and potentially influence the subsequent fuel loading observed in

571   this study. However, treatments at this scale may be costly and result in removing valuable

572   timber product (Temperli et al. 2014). Silvicultural techniques including tree planting and

573   shelterwood treatments may increase stand resiliency to bark beetle outbreaks by creating

574   favorable microsite conditions to promote spruce regeneration (DeRose and Long 2014). More

575   broadly, post-disturbance tree planting may promote stand resiliency and the persistence of

576   subalpine species on the landscape, though long-term patterns of tree regeneration are unknown

577   given the centuries long recovery time scale.

578   *Conclusions*

579   Climate change is altering forest disturbance regimes, which are corresponding with

580   heightened canopy mortality (Allen et al. 2010, Johnstone et al. 2016). An increase in the extent

581   of disturbances will inevitably result in an increase in the interactions of disturbance events.

582   Despite disturbance interactions and presence of tree regeneration on all studied sites, low post-

583   fire seedling density following wildfires, regardless of previous outbreaks, is consistent with

584   other studies in the Rocky Mountains (Harvey et al. 2016*a*; Stevens-Rumann et al. 2018). While

585   this study did not support compounded or additive effects from interacting disturbances, low

586   post-fire Engelmann spruce and subalpine fir regeneration in the Rocky Mountains may promote

587   structural shifts to favor drought- and fire-tolerant species such as lodgepole pine and aspen.

588   Continued high severity disturbance events may reduce forest resiliency and result in state shifts

589   to altered forest types or non-forested ecosystems, particularly in slow-growing subalpine stands

590   (Gill et al. 2017; Turner et al. 2019; Andrus et al. 2020).

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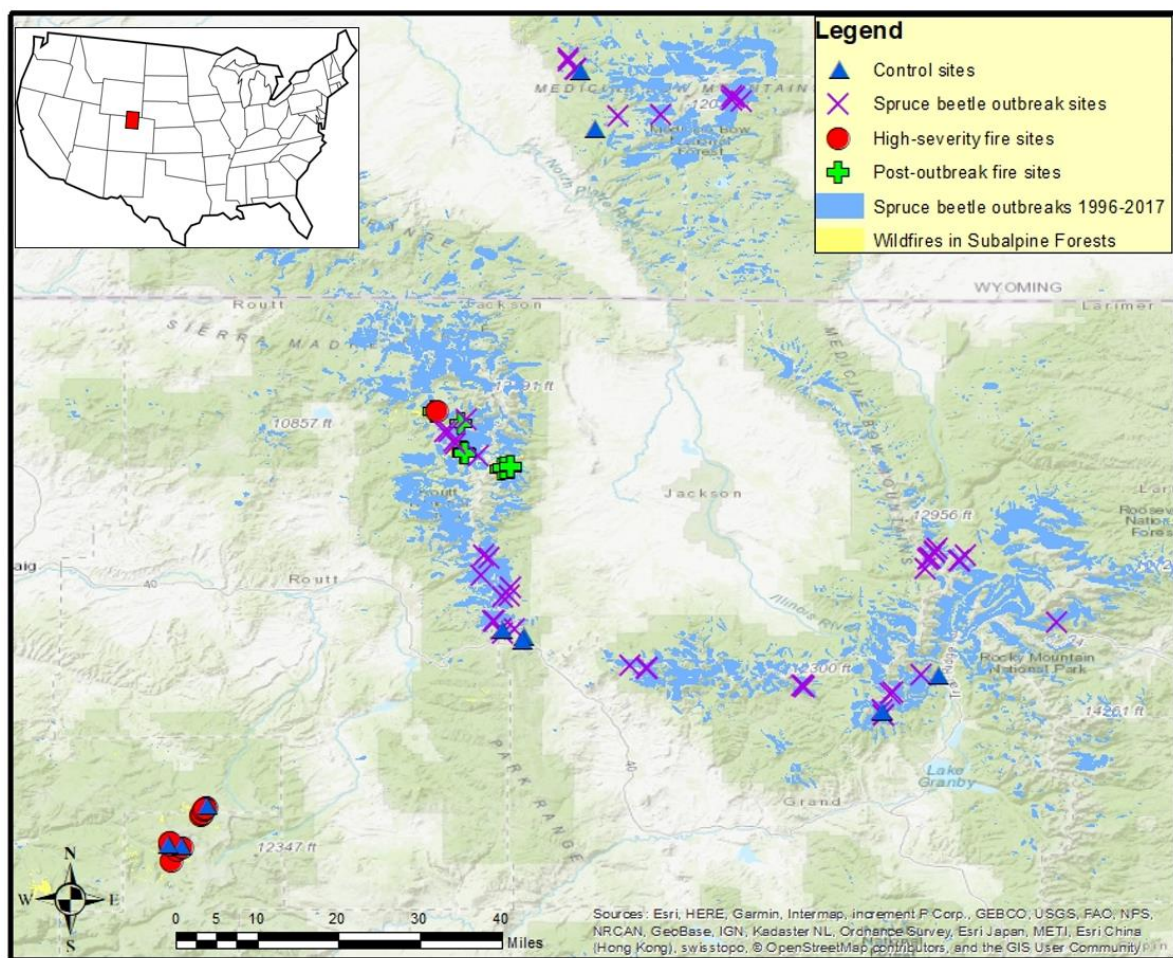883

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FIGURES AND TABLES

Table 1: Predictor and response variables used in analyses for each study question.

Study question	Predictor variables	Response variables
Question 1) how does time-since-outbreak affect stand and fuel structures in subalpine forests?	Time since outbreak	Engelmann spruce mortality Snag density Live tree density 1hr 10hr 100hr 1000hr Total fuel loading
Question 2) how does the recovery trajectories and fuel complexes differ between wildfires, outbreaks, or a combination of the two disturbances?	Disturbance groups: Bark beetle, control, high severity fire, and post-outbreak fire	Litter and duff 1hr 10hr 100hr 1000hr Understory vegetation cover Seedling density (by species) $(\log_{10}(\text{density}(T/ha)))$
Question 3) what are the site specific drivers of post-disturbance fuels and tree regeneration?	Elevation Aspect Slope Disturbance group Fuel loading Litter cover Standing pre-fire species (T/ha)	1hr 10hr 100hr 1000hr Total fuel loading Seedling density (by species) $(\log_{10}(\text{density}(T/ha)))$

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Figure 1: Map of study sites in Northern Colorado and Southern Wyoming.
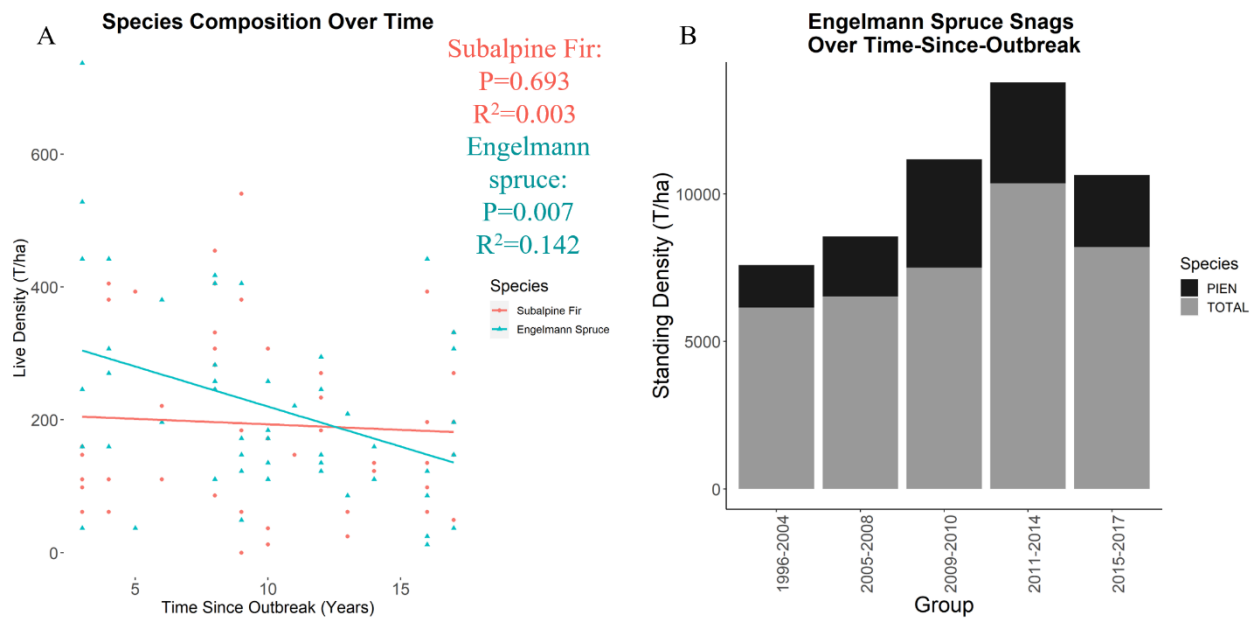
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Figure 2: Standing Engelmann spruce dynamics in beetle-affected sites. A) Live standing Engelmann spruce and subalpine fir over time since outbreak. B) Standing Engelmann spruce snags density compared to total standing tree density. Snags shown as a proportion of total standing trees. Some living trees in total standing density were beetle infested and will die over time.

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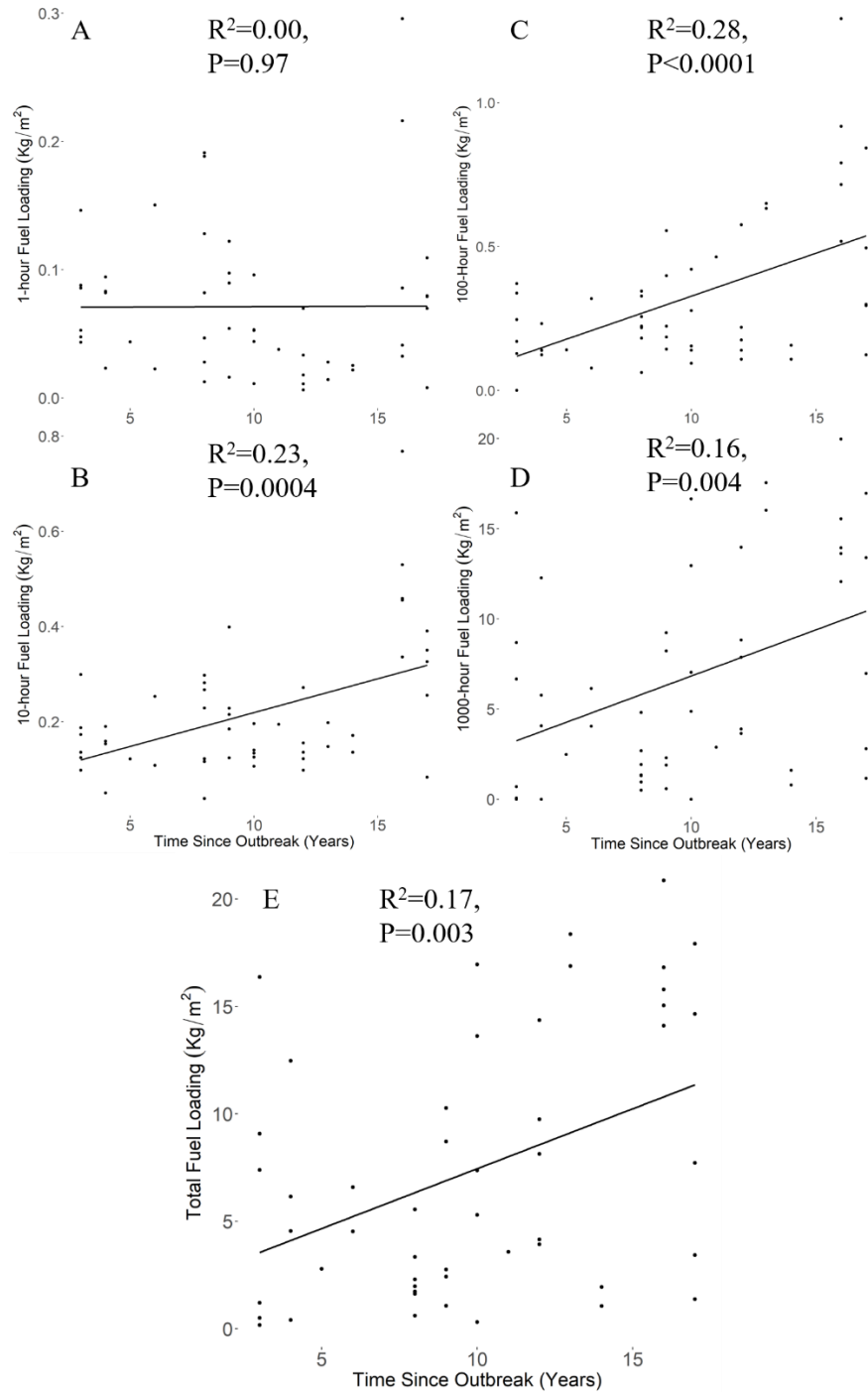
Figure 3: Fuel loading (Kg/m^2) over time in spruce beetle-affected subalpine stands with fitted

linear regression. A) 1-hour fuel loading over time; B) 10-hour fuel loading over time; C) 100-

hour fuel loading over time; D) 1000-hour fuel loading over time; E) Total fuel loading over
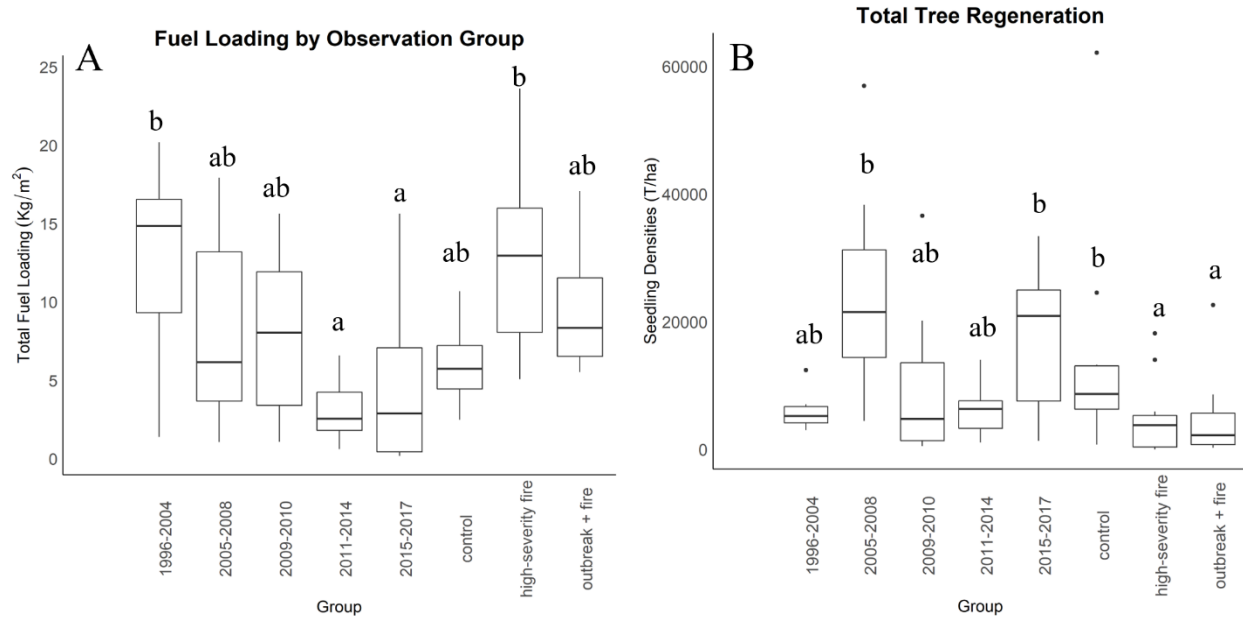
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Figure 4: A) Boxplots of total fuel loading by group. B) Boxplot of total tree seedling densities

including all species in each disturbance group. Horizontal bars represent mean fuel loading of

each disturbance group, height of boxes represent spread of 75% of data. Different letters

indicate statistically significant differences between groups from a Tukey's HSD analysis; B)

analyses were conducted on log-transformed seedling densities; raw densities are graphically
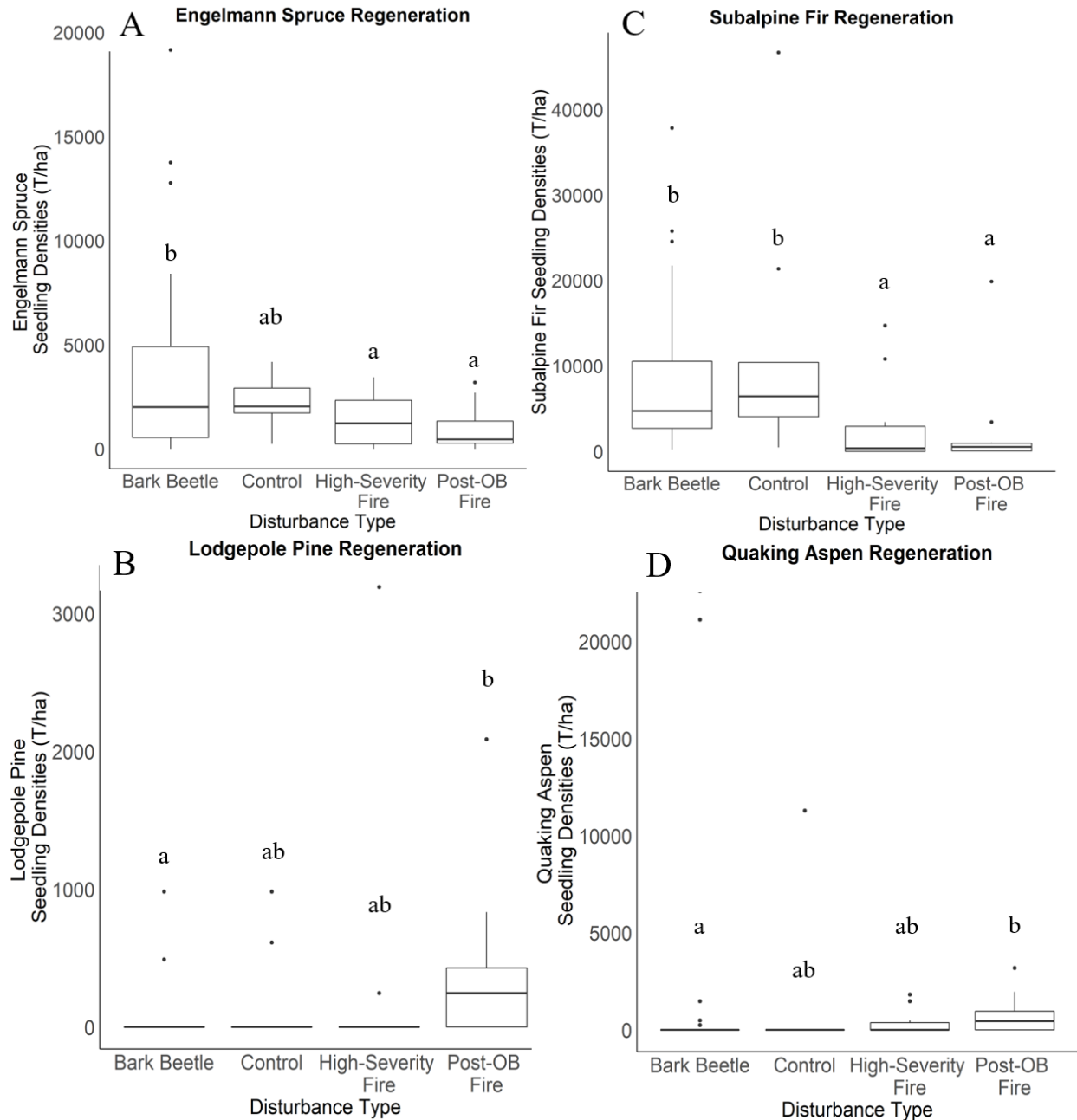
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Figure 5: A) Engelmann spruce, B) Subalpine fir, C) Lodgepole pine, D) Quaking aspen tree seedling densities by disturbance type. Lowercase letters indicate significant differences observed among disturbance types using Tukey's HSD test on log-transformed seedling densities; raw densities are graphically displayed.
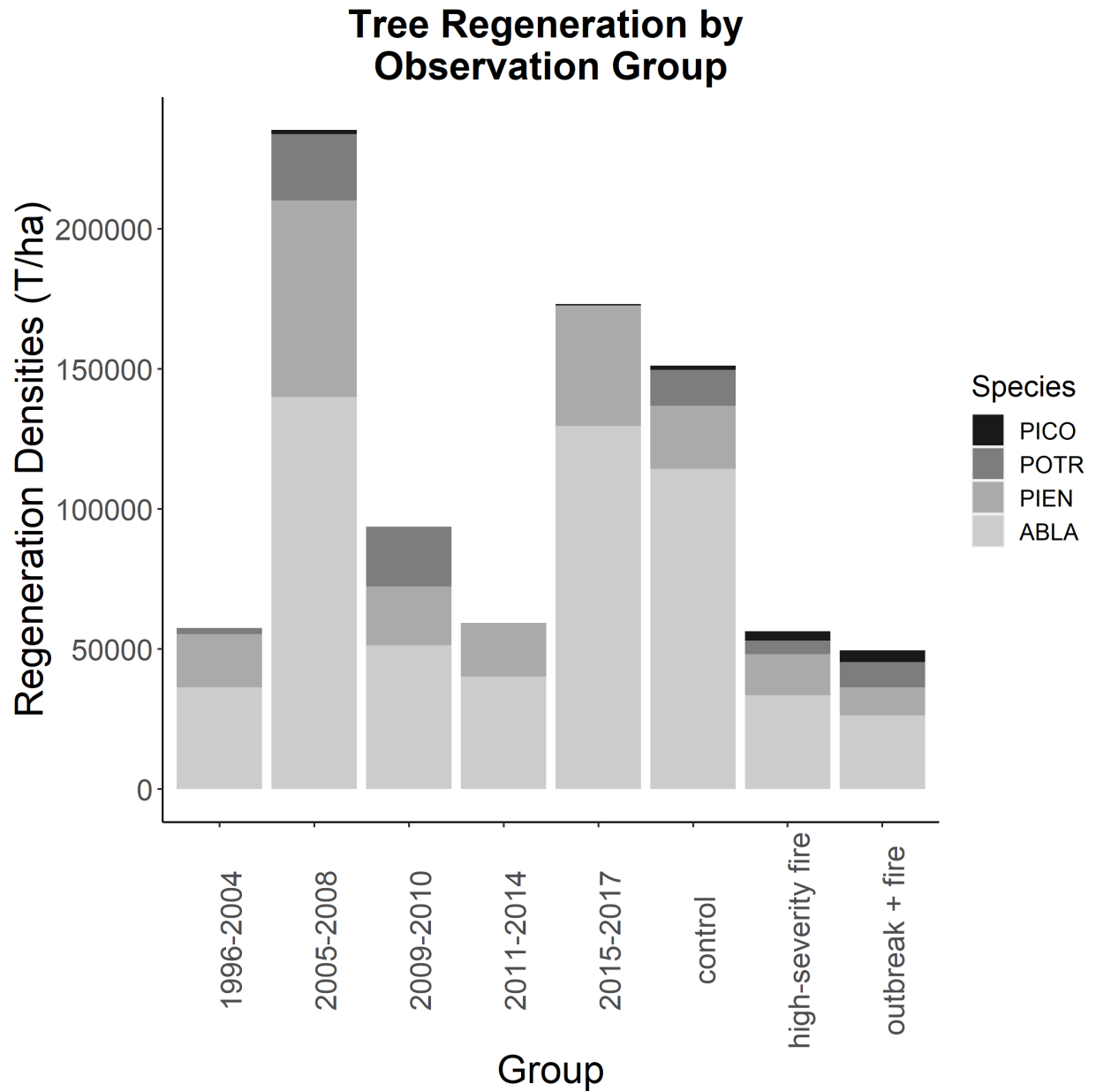
Tree Regeneration by Observation Group

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Figure 6: Tree seedling densities for each species by observation group. Seedling densities are log-transformed.

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